THE GENUS LYCURUS (GRAMINEAE) IN NORTH AMERICA

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LYCURUS was described by Kunth (1816) from Mexican collections made by Humboldt & Bonpland in 1803. The plants were said to be similar to Phleum in habit, and related to Aegopogon. He commented on the paired spikelets (one hermaphroditic and borne on a longer pedicel; the other staminate or neuter), and the first glume which is not only 2-nerved but bears two, or rarely three, awns. Two species were described: L. phleoides from central Mexico, and L. phalaroides from the southwestern part of the country. Although rather lengthy descriptions are included for both species, the most diagnostic features seem to be: culms erect and ligule "abbreviata, fissa" for L. phleoides, versus culms ascending and ligule "brevissima, glabra" for L. phalaroides. In a later work, Kunth (1829) seems to have taken a different view with regard to the relationship of his new genus. At the end of a rather lengthy generic description, one finds: "Hinc Muhlenbergiae, inde Cinnae proxime affinis." A. S. Hitchcock (1920) selected L. phleoides as the type species of the genus, indicating that the choice was based on the fact that it was illustrated in H.B.K.; there was no illustration of L. phalaroides in that work.

The type specimens of the original Kunth species, which I was able to examine at the Paris Herbarium, are both somewhat incomplete; neither has a true base. For the general habit, therefore, we must rely primarily on the original descriptions: "culmo ascendente . . ." for L. phalaroides; "culmo erecto . . ." for L. phleoides. Whereas the inflorescences are rather similar in the two, there are vegetative differences. In L. phleoides the ligule is 1--2 mm long, consisting of two evident "sheath auricles" on either side of a slightly shorter erose middle portion. The blades are mostly acute at the apex. In L. phalaroides, in contrast, the ligule is a small inconspicuous scale about 0.5 mm long. It is as Kunth indicated: "brevissima, glabra." The somewhat shorter blades are navicular at their tips.

Some three decades after the original publication of Kunth's genus, Nuttall (1848) focused on the paired spikelets in plants collected in the vicinity of Santa Fe [New Mexico] in 1841 by Wm. Gambel. When Nuttall observed that all of the spikelets had perfect flowers, he felt the need to describe a new genus and species: Pleopogon setosum. The diagnosis ends: "Allied apparently to Lycurus but the flowers are all hermaphrodite." Bentham (1881), without comment, placed Pleopogon setosum as a synonym of Lycurus phleoides, where it has remained for more than a century.

The only additional novelties described in the genus are those of Beal (1896). He states (p. 270): "There are two species [of Lycurus] found in Mexico so nearly alike that it is difficult to

distinguish one from the other. Following a suggestion of Bentham, I make one a mere variety of the other." Actually, he did not make the combination, nor did he even mention L. phalaroides by name. He listed Nuttall's genus as a synonym, but misspelled it Cleopogon. He proposed two varieties for L. phleoides: var. glaucifolius and var. brevifolius. The former was based on plants collected on rocky hills near Chihuahua, Chi., Mexico, May 28, 1885, by C. G. Pringle (no. 426). Mrs. Chase noted (on an interleaf in Hitchcock's MEXICAN GRASSES) that this variety "looks different, but is only a robust specimen." Beal's second variety, var. brevifolius, was based on another Pringle collection (no. 2470) from the plains of Guadalajara, Jal., Mexico, Oct. 23, 1899. This appears to represent L. phalaroides, the type of which originated in nearby Michoacan.

Kunth's original statement that the upper spikelet of the pair is hermaphrodite, the lower staminate or neuter, has been repeated by several American botanists. Indeed, McVaugh (1983) states: "Spikelets one-flowered, in pairs, the lower of the pair sterile, the two falling together." Examination of numerous specimens of Lycurus, however, reveals that whereas many of the pairs of spikelets are as Kunth described them, there are, nevertheless,others in which both spikelets are fertile, some in which both are staminate or neuter, and still others in which the lower spikelet is hermaphrodite and the upper neuter. A survey of 100 pairs of spikelets from Mexican plants revealed that 65 had the upper fertile, the lower staminate or neuter; 18 had both spikelets fertile; and in 17 the upper spikelet was neuter and the lower fertile. In another examination of 63 pairs of spikelets from three collections made in Arizona, we found among the lower spikelets 26 fertile, 13 staminate or sterile; upper spikelets 22 fertile, 16 staminate or sterile; and in 14 both the upper and lower spikelets were fertile. It is of interest that Bentham & Hooker (1883) indicated that contrary to Kunth's statement, they found that both spikelets of a pair may be fertile, or both sterile.

An accurate description of the inflorescence of members of the genus Lycurus should indicate that it is a dense spicate panicle in which the spikelets are borne in pairs (rarely in threes) on short unequal pedicels. The pedicels are essentially discrete to the point of attachment to the rachis, but may be more or less fused together at their bases. The zone of abscission is at the base of the pedicels, the spikelets often falling as a group, but may later separate. The dehiscence of the spikelet pair leaves a short stump on the main panicle axis, revealing a spiral arrangement of the branchlets. The spikelets may be fertile or staminate or neuter. The first glume is usually 2-nerved and 2-awned (the awns may be unequal in length); the second glume has one nerve which extends as a flexuous awn slightly longer than the body. The glume features are sufficiently variable to make the use of nervation, shape, etc. of little value in keying the species. The florets consist of a 3-nerved lemma, the mid-nerve extending as a flexuous awn about as

long as the body, which is short pubescent along the margins; the palea is 2-nerved and short pubescent on the back; the pale stamens are 1.7--2 mm long.

Hitchcock (1913) in his MEXICAN GRASSES, listed the two Kunth species of Lycurus, along with L. phleoides var. glaucifolius Beal (1896). The key is based on the presence of one awn on the lower glume (L. phalaroides), versus two nearly equal awns (L. phleoides). That this separation is less than satisfactory is seen from the fact that the key statement for L. phalaroides is qualified by "and often a second shorter awn," [on the lower glume]. Beal's variety was said to have scabrous culms and firm, glaucous blades. The specimens cited indicate that both species are widely distributed throughout Mexico, with the variety confined to Chihuahua and Durango. This treatment suggests that Hitchcock paid insufficient attention to the original descriptions, in which the glumes are said to be unequal, the lower somewhat longer, 2- or rarely 3-fid in the generic characterization, as well as being restated in the detailed description for each species. Moreover, a type fragment of L. phalaroides (at US) clearly shows two unequal awns on the lower glume. The shorter awn varies from 0.5--1 mm; the longer, 1.5--2 mm. The differences in size, habit, and ligule given by Kunth in the original descriptions for the two species, were not mentioned in the 1913 Hitchcock work.

In the NORTH AMERICAN FLORA, Hitchcock, et al. (1937, 1939) continued to recognize both of Kunth's species, and placed Pleopogon setosum, along with L. phleoides var. glaucifolius as synonyms of Lycurus phleoides. In this work they seem to have abandoned any attempt to use inflorescence characters, and instead rely on the vegetative differences pointed out by Kunth. In their key, the culm is said to be erect or decumbent, vs. decumbent spreading; and the ligule 2--3 mm long, visible from the side, vs. short and inconspicuous. The range of L. phleoides is given as extending into western United States; that of L. phalaroides as confined to Mexico (and southern South America). Essentially the same morphological distinctions mentioned above were utilized by McVaugh (1983) in separating the two species of Lycurus.

I. M. Johnston (1943) included Lycurus phleoides among the plants found in the states of northern Mexico with which he was concerned, and listed L. phleoides var. glaucifolius as a synonym. He added: "Hitchcock . . .(1913) reports L. phalaroides H.B.K. from Cedros, Zac. (Lloyd 179). The report needs verification. Perhaps a slender specimen of L. phleoides is involved." I have examined the Lloyd specimen mentioned (at US), and it fits my concept of L. phleoides, since it has auriculate ligules 2--3 mm long. The comment by Johnston suggests that he accepted the two Kunth taxa as distinct species.

It seems clear that in Lycurus there are no good inflorescence characters which can serve to separate taxa. As others have found in studying critical groups, it is often essential to rely heavily

on vegetative characters in classification. McVaugh (1983), one of the most recent authors to deal with this problem, states (p. 224): "I can find no spikelet-differences that correlate with these differences in vegetative characters." Overemphasis on floral (inflorescence) features may have prompted Mrs. Chase to write on the interleaf opposite the key on page 304 of Hitchcock's MEXICAN GRASSES (1913) [copy in the Hitchcock-Chase Library at US]: "A.C. [Agnes Chase] examined spklts. of types and compared HBK descriptions. Differences do not hold at all. All one species, the equal and unequal glumes long or short; culms smooth, scabrous or almost canescent--nothing holds. The type specimen of var. glaucifolius looks different, but it is only a robust specimen. [signed] AC August, 1940." Many of the "grass types" at US are merely inflorescence fragments--often only a few spikelets. This is true for Lycurus, except for the Beal varieties. For L. phalaroides there is also a disarticulated leaf.

Chromosome numbers, which in other genera are often useful in segregating taxa, are of little value in this group. Recorded counts are 2n = 40, or ca. 40 (Avdulov, 1931: Gould, 1964,1965; Reeder, 1967, 1971, 1977). Brown's (1951) record of 2n = 28 for a Texas collection is suspect, and although he expressed skepticism of an x = 7 count for an assemblage of dry-land plants, he seems to have made no further effort to check this. Gould (1965) commented on irregularities in meiosis, with frequent univalents and multivalents in his preparations. Reeder (1967) also reported meiotic irregularities.

Apparently after 1940, at US all collections of Lycurus from the USA and Mexico were determined as L. phleoides. However, this "lumping" has not been accepted by all workers, e.g. I. M. Johnston (1943), Pilger (1956), and McVaugh (1983).

As we have observed Lycurus in the field throughout its range in Mexico and southwestern USA, and studied numerous herbarium collections, it is difficult to believe that it is all one highly variable species. In fact, I have concluded that what is represented is not two species, as the author originally proposed, but three. Kunth, of course, did not see material from northern Mexico, nor from the southwestern United States. In addition to the original two species, which are separated by habit and leaf characters, a third northern element exists which can be characterized by its densely caespitose habit, rigidly erect culms, elongate blades, and delicate hyaline ligules 5--6 (rarely to 10) mm long. In dried specimens these delicate ligules are often bent back onto themselves, thus appearing shorter than their actual length. One of the more interesting features of this taxon is that the upper culm blades terminate in a slender scabrous seta 2--6 (-10) mm long. These setae are somewhat fragile and may be broken if care is not taken in pressing and preserving the specimens.

A synonym of Lycurus, as referred to earlier, is Pleopogon Nutt., the type of which was collected by Wm. Gambel near Santa Fe, New Mexico. The single species, P. setosum, is universally treated as

a synonym of L. phleoides, and no combination using Nuttall's epithet, setosum, has been made in Lycurus. Since the taxon I view as a third American species of Lycurus is the "northern element" of the genus, a careful look at Pleopogon setosum seemed in order. At US there is a small fragment of the inflorescence, but as indicated earlier, in this genus spikelet features are of little value in differentiating taxa. Locating the actual holotype proved to be something of a problem. One would suppose it would be at PH, or if not there perhaps GH, but such was not the case. Ewan (1981) states, regarding Gambel's collections: "Although references in the literature state that his plants of 1841 are at PH, I have failed to locate one, nor did F. W. Pennell recall any." Ewan adds that Nuttall did not always acknowledge specimens collected by others, and took some of Gambel's specimens to England with his own. This proved to be the case with the type of Pleopogon setosum, as we learned, upon inquiry, that the fragment at US was from a specimen at Kew.

Through the courtesy of the Director at Kew, we obtained the loan of the Gambel specimen. We can only surmise that it was deposited there when Bentham & Hooker were working on their monumental GENERA PLANTARUM, since it is marked "Herbarium Hookerianum, 1867." There is no indication that the material was collected by Gambel, but "St. an Fee. R. Mts." and the Nuttall reference to the original description appear on the herbarium sheet. This specimen consists of a single culm with a couple of axillary branches, but no basal portion. However, several of the blades have setae 4--6 mm long, and the hyaline ligules measure 3--4 mm in length. This specimen clearly represents the taxon I consider worthy of designation as a third species of Lycurus. The appropriate combination is proposed below.

Lycurus setosus (Nutt.) C. Reeder, comb. nov.

Pleopogon setosum Nutt., Proc. Acad. Philadelphia 4: 25. 21 March to 4 April 1848; Jour. Acad. Sci. Philadelphia II. 1: 189. Aug. 1--8. 1848. [cf. Reveal & Spevak, Taxon 16: 407--414. 1967]. Type: USA: New Mexico: mountains near Santa Fe, William Gambel s.n. in 1841 or 1842. (Holotype: K! fragment, US!)

Lycurus phleoides var. glaucifolius Beal, Grasses North Amer. 2: 271. 1896. Type: Mexico: Chihuahua: rocky hills near Chihuahua, 28 May 1885, C. G. Pringle 426. (Holotype: MSC! Isotypes: US! NY!)

Distribution: USA: western Texas and the Panhandle of Oklahoma to New Mexico and Arizona, north to Colorado and Utah. Mexico: from northernmost Baja California to Sonora, Chihuahua, and no. Durango.

Representative specimens: USA: Oklahoma: Cimarron Co., Waterfall 7494 (YU), Demaree 13390 (NY). Colorado: El Paso Co., Reeder & Reeder 5146 (RM); Spanish Peaks, A. Chase 5394 (US); Manitou, A. Chase 5302 (US). Texas: Brewster Co., Chisos Mts., Warnock 814 (ARIZ), Shinners 8771 (ARIZ); Culberson Co., Guadalupe Mts., Moore & Steyermark 3364 (US); Jeff Davis Co., Limpia Canyon, Reeder &

Reeder 4233 (ARIZ,YU). New Mexico: Grant Co., Blumer 150 (NY, US); Socorro Co., Mogollon Mts., Metcalfe 569 (ARIZ, K, NY, US); Organ Mts., Wooton 1056 (US); Santa Fe Co., Glorieta, Bennett 8799 (ARIZ). Arizona: Pima Co., Santa Rita Mts., Peebles & Harrison 2936 (ARIZ), L. N. Goodding 2456 (NY, RM); Rincon Mts., Blumer 3352 (ARIZ); Cochise Co., Dragoon Mts., Adams Ranch, Griffiths 1838 (ARIZ, NY, US); Huachuca Mts., Gould et al. 2426 (ARIZ, NY). MEXICO: Baja California Norte: Sierra San Pedro Martir, Moran 24849 (ARIZ). Sonora: El Tigre, Santos 1952 (ARIZ, K, MEXU, NY, US); La Angostura, Santos 1818 (ARIZ, K, NY). Chihuahua: Sierra Azul, Pennell 18648 (NY); Mapula Mts., Pringle 904 (MEXU, NY); Cuesta Blanca, Reeder & Reeder 3229 (ARIZ); W of Cd. Chihuahua, Harvey 1548 (US). Durango: Sierra Gamon, H. S. Gentry 8322 (GH, US).

The other two North American species which I recognize are listed below, along with synonymy, notes on distribution and citation of representative specimens.

LYCURUS PHLEOIDES H.B.K., Nov. Gen. & Sp. 1: 142. pl. 45. 1816.
Type: MEXICO: "Crescit in temperatis Mexici, inter Guanaxuato et Temascatio et in radicibus aridissimi montis La Buffa, alt. 1030 hexap. Floret Septembri." Humboldt & Bonpland s.n. (Holotype: P! fragment,US!)

Distribution: MEXICO: Coahuila, Nuevo Leon, Tamaulipas, and southern Chihuahua, south to Oaxaca. USA: a few collections from the Trans-Pecos region of Texas, and adjacent eastern New Mexico.

Representative Specimens: USA: New Mexico: Carlsbad, Tracy 8196 (US). Texas: Culberson Co., Guadalupe Mts., Moore & Steyermark 3614 (NY, RM,US), Standley 40574 (US); Big Springs, Tracy 8215 (F, US). MEXICO: Coahuila: Saltillo, I. M. Johnston 7250 (US), Palmer 339 in 1904 (K, NY, US). Durango, near Cd. Durango, Reeder & Reeder 4463 (ARIZ). Nuevo Leon: Galeana, V. H. Chase 7691 (ARIZ, GH, NY, US). San Luis Potosi: San Lorenzo, Reeder & Reeder 2937 (ARIZ); vicinity Cd. San Luis Potosi, Parry & Palmer 939 (US, YU). Guanajuato: Dolores Hidalgo, Reeder & Reeder 2267 (ARIZ). Hidalgo: El Salto, Pringle 9571 (GH, K, US). Puebla: San Marcos, Hitchcock 6535 (ARIZ, US), 6514 (ARIZ,US); Tehuacan, Pringle 6689 (ARIZ, MEXU, US,YU). Oaxaca: Hacienda de Aguilera, Silvio & Conzatti 3604 (MEXU, US).

LYCURUS PHALAROIDES H.B.K., Nov. Gen. & Sp. 1: 142. 1816.
Type: MEXICO:"Crescit in montanis regni Mechoacanensis juxta Valladolid [Morelia], Alberca de Palangeo et Patzcuaro, alt. 950--1060 hexap. Floret Septembri." Humboldt & Bonpland s.n. (Holotype: P! fragment, US!)
Muhlenbergia lycuroides Vasey ex Beal, Grasses North Amer. 2:239. 1896. Type: Mexico: Jalisco: Guadalajara, Palmer 489 in 1886. (Holotype: MSC! Isotypes: MEXU! NY! US!)
Lycurus phleoides var. brevifolius Scribn. ex Beal, Grasses North Amer. 2: 271. 1896. Type: Mexico: Jalisco: plains of Guadalajara, 23 Oct. 1889, Pringle 2470. (Holotype: MSC! Isotypes: GH! MEXU! NY! US!) [Beal cites Palmer 489, the type collection

of Muhlenbergia lycuroides, among the specimens listed for this variety!]

Distribution: MEXICO: southernmost Chihuahua, south to Chiapas and Guatemala, with a few collections from the Cape Region of Baja California Sur.

Representative Specimens: MEXICO: Baja California Sur: Cape Region Mts., Brandegee 25a (US); Sierra de la Laguna, Brandegee 77 (US). Zacatecas: Plateado, J. N. Rose 2794 (K, US). Guanajuato: between Cd. Guanajuato and Santa Rosa, H. E. Moore, Jr. 1350 (US). Jalisco: Guadalajara, Hitchcock 7307 (US), Palmer 459 in 1886 (K, MSC, NY, US). State of Mexico: Temascaltepec, Hinton 1855 (K, NY, US, MEXU). Distrito Federal: Valley of Mexico, 8000 ft., Pringle 6576 (ENCB, MEXU, MSC, NY, US). Michoacan: Uruapan, Hitchcock 6967 (US); Jacuare, Hitchcock 7006 (US). Chiapas: San Cristobal, E. W. Nelson 3228 (US). GUATEMALA: Quezaltenango, Chiquilaja, de Koninck 63 (US).

A few of the collections which I consider to represent L. phalaroides have a short seta on two or three of the uppermost blades. These plants have decumbent to spreading culms, and the ligules are short deltoid or truncate. The blades tend to be shorter in this taxon than in the other two. Two collections are of special interest: Reeder & Reeder 4753 (ARIZ, YU) from Guanajuato is unusually hairy throughout; and Reeder & Reeder 2028 (ARIZ) from Chiapas has many of the glumes (both first and second) with only one nerve and one awn.

Among the large number of specimens examined, only a few proved puzzling. These were collected in areas where the ranges overlap, and may represent possible hybrids or introgressive types.

Key to the species

1. Leaves, at least the upper ones, terminating in a slender seta as much as 10 mm or more long; ligule hyaline, acute to acuminate, (3) 5--6 (-10) mm long; plants caespitose, the culms erect . . . . . L. setosus

1. Leaves without setae, or if with short mucros, then ligules usually 2 mm or less long; plants decumbent, or culms ascending or widely spreading.

2. Ligules truncate or broadly deltoid, mostly 0.5--1 mm long, not or only slightly visible from the side; blade tips navicular, obtuse, or rarely acutish; plants decumbent, or culms widely spreading . . . . . L. phalaroides

2. Ligules 1.5--2 (rarely to 3) mm long, with evident "sheath auricles" on either side; blade tips acute, mucronate, or rarely with short points; culms ascending or lax and commonly geniculate . . . . . L. phleoides

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LITERATURE CITED

Avdulov, N. P. 1931. Karyo-systematische Untersuchung der Familie Gramineen. Bull. Appl. Bot., Genet. & Pl. Br. Suppl. 44. 428 pp.

Beal, W. J. 1896. Grasses of North America. Vol. 2. New York: Henry Holt & Co. 796 pp.

Bentham, G. 1881. Notes on Gramineae. J. Linn. Soc. Bot. (London) 19: 14--134.

_____ & J. D. Hooker 1883. Gramineae. In: Genera Plantarum. Vol. 3. Pt. 2. pp. 1019--1215.

Brown, W. V. 1951. Chromosome numbers in some Texas grasses. Bull. Torrey Bot. Club 78: 292--299.

Ewan, J. & N. D. Ewan 1981. Biographical Dictionary of Rocky Mountain Naturalists: 1682--1932. The Hague: Junk. xvi + 253 pp.

Gould, F. W. 1964. In: Documented chromosome numbers of plants. Madroño 17: 266--268.

_____ 1965. Chromosome numbers of some Mexican grasses. Bol. Bot. Soc. Mexico 29: 49--62.

Hitchcock, A. S. 1913. Mexican Grasses in the United States National Herbarium. Contr. U. S. Natl. Herb. 17(3): 181--389.

_____ 1920. The genera of grasses of the United States with special reference to the economic species. U.S. Dept. Agric. Bull. 772. 307 pp.

_____ 1937, 1939. Lycurus H.B.K. North American Flora 17(7): 542; 17(8): 543.

Humboldt, F. W. H. A. von, A. Bonpland, & C. S. Kunth 1816. Nova Genera et Species Plantarum. Gramineae. Vol. 1 (pts. 1--2): i--lx, 1--144. pl. 1--44 (Jan. 29); (pt. 3): 145--288. pl. 45--70. (Mai); (pt. 4): 289--377. pl. 71--96. (late Aug.)

Johnston, I. M. 1943. Plants of Coahuila, eastern Chihuahua, and adjoining Zacatecas and Durango, II. J. Arnold Arb. 24: 375--421.

Kunth, C. S. 1816. (see Humboldt, Bonpland, & Kunth in this list)

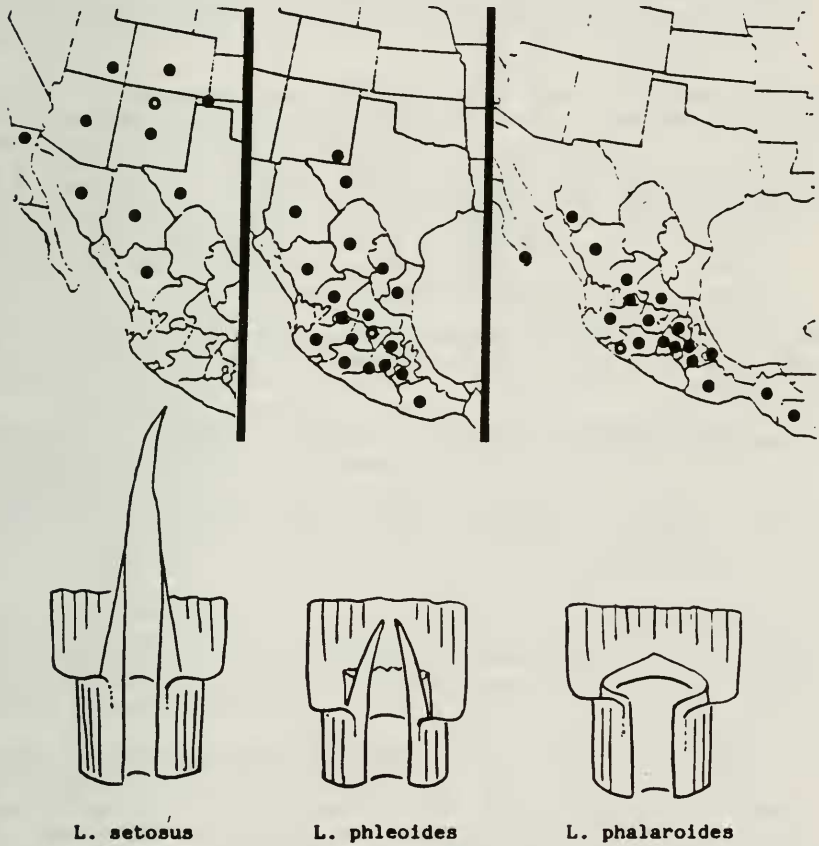
_____ 1829. Revisión des Graminées publiées dans les Nova Genera et Species Plantarum de Humboldt et Bonpland. Paris. [Lycurus, p. 64. June]

McVaugh, R. 1983. Flora Novo-Galiciana. A descriptive account of the vascular plants of western Mexico. Vol. 14. Gramineae. 436 pp. Ann Arbor: Univ. Michigan Press.

Nuttall, T. 1848. Descriptions of plants collected by Mr. William Gambel in the Rocky Mountains and Upper California. Proc. Acad. Philadelphia 4: 7--26. (21 March -- 4 April).

_____ 1848. Descriptions of plants collected by William Gambel, M.D., in the Rocky Mountains and Upper California. J. Acad. Philadelphia Ser. II. 1: 149--180. (1--8 Aug.)

Pilger, R. 1956. Gramineae. In: Nat. Pflanzenfam. ed. 2. 14d. 168 pp.
Reveal, J. L. & V. S. Spevak 1967. Publication dates and current names of 144 names proposed in two 1848 Thomas Nuttall articles. Taxon 16: 407--414.
Reeder, J. R. 1967. Notes on Mexican grasses VI. Miscellaneous chromosome numbers. Bull. Torrey Bot. Club 94: 1--17.
_____ 1971. Notes on Mexican grasses IX. Miscellaneous chromosome numbers--3. Brittonia 23: 105--117.
_____ 1977. Chromosome numbers of western grasses. Amer. J. Bot. 64: 102--110.



Distribution map and a representative ligule for each of the N.A. species of Lycurus. The open circle on a map indicates the type locality for that species.